THE CLASSIFICATION OF THE ARTHROPODA.

By J. S. Kingsley.

(*Continued from page* 135, *February, 1894.*)

Sub-Class II—Eucrustacea.

Crustacea, with filiform, plumose or lamellate gills, in either thoracic or abdominal region; mouth parts never ambulatory in the adult, but modified for the prehension and comminution of food. Nauplius stage either free-swimming or passed in the egg.

It is difficult, with our present knowledge, to find good diagnostic points separating the true Crustacea from the Trilobites, and it may be that further research will show that the latter are to be regarded as a division equivalent to some of those mentioned below. At present, the arrangment of the feet of the cephalic region in a circle around the mouth, the use of their basal joints for the comminution food, and the apparent functioning of the distal joints as locomotor organs, together with the peculiar gills, must serve to differentiate the two groups, it being understood that the ideas here expressed are merely provisional.

In the sub-division of the Crustacea I am inclined to adopt the recent "sub-classes" of Grobben ('92) as super-orders as follows:

Super-Order I, Phyllopoda.
  Order I, Euphyllopoda.
  Order II, Cladocera.
Super-Order II, Estheriæformes.
  Order I, Ostracoda.
Super-Order III, Apodiformes.
  Order I, Copepoda.
  Order II, Cirripedia.
Super-Order IV, Malacostraca sive Branchipodiformes.

I, Leptostraca.
Order I, Nebaliadæ.
II, Eumalacostraca.
Order I, Stomatopoda.
Order II, Thoracostraca.
Order III, Arthrostraca.

On the whole, I accept the conclusions of Grobben as to the relationships of the various groups, and have, like many other zoologists, regarded the Phyllopods as the ancestral stock. I think that this is shown by, among other points, the structure of the appendages, regarding which I fully accept the conclusions of Lankester[2] ('81). I do not regard the nauplius stage as indicative of a naupliform ancestor, but as an introduced feature, for which view the arguments adduced by Claus and Dohrn, seem valid. The ancestor of the Phyllopods must have been an elongate poly-somitic animal with lamellate appendages, the basal portions of one or more "legs" serving at the same time as both locomotor and manducatory organs. In short, my views as to the ancestral form are much like those adopted by Bernard ('92), although I cannot accept all of his conclusions as to the steps of the evolution.

Class II—Acerata.

Branchiate Arthropods, in which the branchial folds, developed from the abdominal appendages function as gills, as lungs, or as tracheæ. The body is divided into cephalothorax and abdomen, the line passing behind the sixth pair of appendages. The genital ducts open upon the first abdominal somite. The anterior postoral ganglia unite to form a ganglionic ring aronnd the œsophagus; the median eyes are in-

[1] I regard Packard's ('87) Syncarida as a group of Amphipoda of scarcely more than family rank.

[2] Grobben does not accept Lankester's views, and claims that embryology shows that Lankester's sixth endite is the endopodite and the flabellum the exopodite, in support of which he cites the observations of Claus ('73, p. 20). I cannot find there or anywhere else in Claus' paper any evidence which is not capable of being interpreted in full harmony with Lankester's view that the 5th and 6th endites of the Phyllopod limb are endopodite and exopodite respectively, while the flabellum is the homologue of the epipodite of the "typical" Crustacean limb.

vaginate. The entoderm (at least in several types) arises by delamination; there is a large mid-gut, with well-developed glands ("liver") while the proctodeum is short. The genital glands are reticulate and the spermatozoa are motile.

There is little to be said upon the foregoing points, to which many more, applicable to both Xiphosures and some Arachnids, might be added. The exact serial correspondence of the respiratory metameres in Limulus and the Scorpions have been enlarged upon by Lankester ('81[a]), and considerable emphasis must be placed upon the fact that in all Arachnids the stomata are ventral, and are, in all instances, except in possibly the Solpugids and a few mites, are confined to the abdomen. These exceptions need new study. In the Scorpion, as in Limulus, the observations of Narayanan ('89) and Laurie ('90) show that the genital ducts are modified nephridia, and that they open upon the posterior surface of the first abdominal appendages. Delamination has been shown to occur in the Pseudoscorpions, Araneina, Phalangids and Limulus, as well as in the doubtfully Arachnidan Pycnogonids.

Sub-Class I—Gigantostraca seu Merostomata.

Six pairs of cephalothoracic limbs around the mouth, the bases of the posterior pairs being masticatory. Behind the mouth a metastomial plate or pair of plates. Anterior edge of carapax acute, its upper surface bearing median ocelli and a pair of lateral compound eyes. Respiration by means of lamellate branchiæ (gill books) borne on appendages 2–6 of the abdomen and protected by the enlarged first pair (operculum) which covers them.

To these points, which cover both Xiphosures and Eurypterids, the following, derived from Limulus, may be added: No salivary glands, no Malpighian tubes, no embryonic membranes (amnion).

In this sub-class two orders are to be recognized, the Eurypterida (fossil) and the Xiphosures. In the latter are included the recent and fossil Limuloid forms. The difference between these is not readily formulated, but is readily recognized in the specimens. The affinities of Cyclus are uncertain.

Order I—Xiphosura.

Cephalothorax large, metastoma paired, telson elongate and spiniform,

Sub Order I—Limulidæ.

Abdominal somites six, coalesced.

Sub-Order II—Hemiaspida.

Abdominal somites more than six, free.

Order II—Eurypterida.

Cephalothorax small, abdomen large and elongate, twelve-jointed, the joints free, telson spatulate, metastoma unpaired.

Sub-Class II—Arachnida.

Respiration by internal lungs or tracheæ, no compound eyes Entodermal Malpighian tubes present; Embryonic membrane (amnion) present in some.

I regard the Scorpionida as the most primitive type of Arachnida existing to-day, and the Acarina as the farthest removed from the original stem. This position of the Scorpions is shown by many facts of structure; and the pulmonate type of respiration—intermediate between the gills of the Gigantostraca and the tracheæ of the higher Arachnids—occuring in these forms is just what we should expect if the line of descent is, as here maintained, from branchiate forms. On the other hypothesis of a common origin of all "Tracheates" from some Peripatoid form, we should have the strange spectacle of the most primitive of all Arachnids with the most differentiated respiratory system.

In the Arachnida I recognize the following orders:[3]—I, Scorpionida; II, Thelyphonida; III, Araneida, IV, Solpugida;[4] V, Pseudoscorpii; VI, Phalangida; VIII, Acarina.

It is interesting to note in this connection that Pocock, on morphological grounds points out (Ann. & Mag, Nat. Hist., VI,

[3] In this I follow the order of Pocock (Ann. & Mag. N. H., Jan., 1893). His "sub-classes" Ctenophora, Lipoctena and super ordinal divisions Chaulogastra, Mycetophora and Holostomata are hardly to be regarded as of phylogenetic value.

[4] No group of Archnids will better repay study than this. I do not believe that the distinction between the "head" and the "thorax" with its three distinct somites indicates any affinities with the Hexapods, but that the conditions here existing are to be best explained upon the ground of homoplassy. The position of the anterior stigmata in the first thoracic somite is of great interest,

xi, p. 2) that "the immediate ancestor of the Arachnida was constructed somewhat as follows: The body was composed of eighteen somites, the anterior of which were provided with large appendages set apart for locomotion and the prehension and mastication of food; the terga of this cephalothoracic region were fused to form a single shield or carapace, supporting a submedian and a cluster of lateral eyes at each side, and the ventral surface of the carapace [? cephalothorax], at least in its posterior half, was protected by a sternal plate. Each of the succeeding six somites bore a pair of small ventral appendages, and the generative aperture opened upon the sternal area of the first of these somites. The posterior six somites had lost their appendages, were probably narrower than the rest, and constituted a limbless caudal portion of the body, the last of them being furnished with a single plate, articulated above the anal aperature." This should be compared with one of the Eurypterida.

Sub-Phylum II—Insecta sive Antennata.

Arthropods with differentiated head consisting of procephalic lobes and four (five[5]) somites; head with somites anchylosed and provided with four pairs of appendages modified for sensation or for feeding; respiration by means of tracheæ (modified glands) opening to the exterior on the sides of the body in the post-cephalic region. Nephridia absent, except as genital ducts, which open near the posterior extremity of the body. Ectodermal Malpighian tubes present. Spermatozoa motile.

So far as I am aware, the dissolution of the old group Myriapoda and the union of the Chilopoda with the Hexapoda was first proposed by Pocock ('87). At about the same time, I taught the same view to my classes, and later ('88) published the same. Subsequently both Pocock ('93) and I ('93, p. 248 ff.) repeated our views within a month of each other.[6] This step, it seems to me, is fully justified. The affinities of the Chilopods to the Hexapods are most close, while those of Chilopoda and

[5] See p. 125.

[6] One of our best students of the Myriapoda, the late C. H. Bollman, accepted my views and they appear in the posthumous collection of his papers ('93).

Chilognatha are quite obscure. There has been no greater stumbling-block for morphologists than the attempt to homologise the somites of millipeds and centipedes. Attempts to bring other organs into harmony are equally futile. The three groups under discussion may be contrasted as follows, it being of course admitted that we know next to nothing of the somites and serial homologies of either Diplopod or Chilopod, and that possibly future research will modify some of the statements below.

The Diplopod head bears, besides the antennæ, but two pairs of appendages—a pair of mandibles and a lower lip, composed of a pair of coalesced maxillæ.[7] In the Chilopod the conditions are as in the Hexapod, two pairs of maxillæ being present.

In the Chilopods, as in the Hexapods, each somite bears a single pair of appendages, while in the Diplopods the majority of the segments bear two pairs of appendages, and the researches of Heathcote ('88) show that each segment is, in reality, composed of two coalesced somites, a condition without parallel elsewhere in the Arthropoda. In the Chilopods there is a wide sternum separating the coxæ of the ambulatory appendages; in the Diplopods the coxæ are approximate, and the sternum is exceeding narrow, or even entirely absent.

In the Chilopods the stigmata, a pair to a somite, are lateral (dorsal in Scutigera), and are placed above and outside the insertion of the limbs, exactly as in the Hexapods. The tracheæ which arise from them are branched, and the intima is thrown into a well-developed spiral thickening as in the six-footed insects. In the Diplopoda, on the other hand, the stigmata are beneath the body[8] close to the legs, while the tracheæ (ex-

[7] The attempt made to show that this lower lip is composed of the two coalesced lower jaws, or first and second maxillæ, of the Chilognaths receives no support from the embryology of Julus (Heathcote '88), where there is but a single somite when the hypothesis calls for two. Further the innervation of the sense organs of the lower lip (*cf.* vom Rath, '86, Pl. XX, Fig. 1) shows that but a single pair of appendages is concerned in the part.

[8] In former papers I have said that the spiracles might be even *in* the coxæ. I recall having seen this statement but recently rather rather extensive reading of Myriapod literature fails to reveal my authority.

cept in the Glomeridæ) are tufted and unbranched, and the thickening of the intima is poorly developed.

In the Diplopods there are well-developed foramina repugnatoria upon the sides of each somite of the body. Such structures are absent from the Chilopods (as from the Hexapods), except in a few Geophilidæ, where repugnatorial glands occur, opening by foramina in the mid-ventral line.

In the Chilopods the reproductive organs consist of paired[9] gonads situated above the alimentary canal and opening to the exterior by ducts which are at first paired, but which later unite into a common tube which leads to a single external opening situated in the penultimate segment of the body. In the Hexapods the conditions are almost exactly the same; the gonads are dorsal, the genital ducts unite (except in Ephemeridæ), and there is a single external opening, always at the posterior end of the abdomen. In both Hexapods and Chilopods the spermatozoa are motile. In the Diplopods there is a single unpaired gonad, situated beneath the alimentary canal, and the genital duct, passing forward, divides into two, each of which has its own opening at the bases of the legs of the second post cephalic segment. The spermatozoa are quiescent.

We know so little of the embryology of the Myriapods that the aid of development can be had to only a slight extent in our comparisons,but the facts which it affords seem important. In the Chilopods the embryo escapes from the egg with numerous ambulatory appendages, a pair to each somite. The same is true of the typical Hexapods, all later observers agreeing that a polypod precedes a hexapod condition. The young Diplopod escapes from the egg in a Hexapod condition, and the presence of these six legs has been seized upon as a proof of the near association of these forms. An exact comparison, however, seems to show that the two are in reality very unlike as appears in the following table.[10]

[9] Single in Scolopendra.

[10] As nothing is known of the existence of a tritocerebral segment in the Diplopods, the comparison can only be made upon the basis of the appendages of the adult. If the tritocerebral segment should prove lacking in the millepeds, the contrast will prove stronger than it now is. The statement of the Diplopod appendages is based upon Heathcote ('88).

	Hexapoda (+Chilopod).		Diplopod.	
Appendage I	Antenna	Head	Antenna	Head
" II	Mandible		Mandible	
" III	Maxilla 1		Lower Lip	
" IV	Maxilla 2		Foot 1	
" V	Thoracic Foot 1	Thorax	Absent	
" VI	Thoracic Foot 2		Foot 2	
" VII	Thoracic Foot 3		Foot 3	
" VIII	Abdominal Foot 1		Absent	
" IX	Abdominal Foot 2		Absent	

Class I—Chilopoda.

Insecta with elongate depressed body, no differentiation between thorax and abdomen, all the somites being provided with appendages, those of the thorax-abdomen being locomotor in function.

Class II—Hexapoda.

Insecta with body consisting of not over 19 somites, divided into head, three-jointed thorax and abdomen. Thorax provided with three pairs of locomotor appendages, and usually with two pairs of wings; abdominal appendages usually lacking from most somites, those of the extremity being usually modified for reproduction and sensory purposes, those of the other somites, when present, being weak.

Sub-Phylum III—Diplopoda sive Chilognatha.

Elongate, homonomously segmented Arthropods; head distinct, bearing three pairs of appendages; no distinction between thorax and abdomen; this region with numerous somites, all, except the anterior, having two pairs of appendages (double somites), sternum narrow. Stigmata two to each somite, tracheæ tufted and unbranched, not anastomosing. Gonads single, beneath the alimentary canal; spermatoza quiescent; genital ducts opening between the bases of the second and third pairs of feet.

I have given above my reasons for the separation of the Diplopods from the Chilopods, and need not repeat them here. I do not discuss the relations of the Diplopoda to the other sub-phyla, nor the relative position to be accorded the group. The ventral position of the gonads is a mark of low rank, but in other respects the organization is much higher.

ARTHROPODA OF UNCERTAIN POSITION.

I—Pycnogonida sive Pantopoda.

Regarding the systematic position of these forms I cannot add anything to the remarks of Morgan ('90), who has shown that not only in adult structure but in certain features of development, notably in the formation of the entoderm by delamination, they present conditions not easily paralled outside of the Arachnida, and it is not impossible that they may belong there. The appendages are easily homologised in the two groups, and especially interesting is the fact that while most genera in the female retain a primitive condition in having the genital ducts open upon several pairs of appendages (IV–VII), in a few these openings occur only on the seventh appendage, exactly where they occur in the Scorpions.

II—Linguatulina.[11]

These forms, frequently associated with the Arachnids, possess but few points of similarity with them. Chief among these are the concentration of the nervous centres to a circum-œsophageal ring, and the peculiar arrangement of the ovarian follicles. On the other hand, neither embryos nor adult resemble any Arachnids in more than a few superficial features. The opening of the genital ducts in the female near the posterior end of the body is not Arachnid in character, nor is the absence of "liver" lobes from the mid-gut. Besides, as non-Arthropodan characters, may be mentioned the extensive cœlom and the outer circular body muscles. The species of Pentastomæ have been so modified by parasitism that it is

[11] Upon points of structure and development consult Stiles ('91) and Spencer ('92), in addition to the older literature.

difficult to say whether the lack of other structures characteristic of Arthropods is due to primitive simplicity or to degeneration.

III—Pauropoda.

The position of the Pauropoda is, as yet, very uncertain, as we are almost entirely ignorant of their internal structure. In the tendency towards a fusion of somites, in the lack of a second pair of maxillæ, and in the positions of the external paired openings of the genital ducts at the base of the second pair of ambulatory appendages and the non-motile spermatozoa they show undoubted affinities with the Diplopoda; but the peculiar triramous antennæ and especially the characters of the hexapod young, as figured by Lubbock ('67) and Ryder ('79) show important differences. The following table compares the somites of Pauropus and the Diplopod:

	Diplopod.	Pauropod.
Appendage I	Antenna	Antenna
" II	Mandible	Mandible
" III	Lower Lip	Lower Lip
" IV	Foot 1	Absent
" V	Absent	Foot 1
" VI	Foot 2	Foot 2
" VII	Foot 3	Foot 3

IV—Tardigrada.

Elongate metameric animals with four pairs of appendages, each terminating with two double hooks. Mouth and anus terminal, Malpighian tubes present, opening into the hind-gut. Nervous system consisting of a supraœsophageal brain and a chain of four ventral ganglia. No specialised circulatory or respiratory organs. No coxal glands or nephridia. Sexes separate, gonad unpaired, emptying into hind-gut.

Most frequently the Tardigrades are associated with the Arachnida, but this has doubtless been due to the possession of four pairs of functional legs in the two groups. These forms

differ from the Arachnids in the absence of all mouth parts,[12] in the proctodeal excretory tubes, the simple nervous system, smooth muscular tissue, and in the absence of nephridia, and they further differ from not only the Arachnids, but from all Arthropods in the fact that the gonads open into the hind-gut.

V—Malacopoda.[13]

The Arthropodan features of the Malacopoda, represented by the single genus Peripatus, are the tracheæ, the legs terminating in claws, the appendicular nature of the jaws, the exclusive use of a pair of nephridia for genital ducts, the reduced cœlom; the several ostia of the heart, the heart being enclosed in a pericardium; the lacunar circulation. On the other hand, the Malacopoda differ from all other Arthropoda and agree with the Annelids in the following particulars:

The presence of functional nephridia in each body segment; the presence of well-developed coxal glands; the existence of an outer circular muscular layer in the body wall; the absence of striation from all muscles except those of the mouth parts; the presence of cilia in the alimentary canal and in the nephridia; the situation of the antennæ as outgrowths from the primitively preoral region; the muscular nature of the pharynx, unlike that of any Arthropod and strikingly that of certain Chætopods. The eyes are too unlike the usual organs of any other Arthropod, but, as figured by Balfour, they closely resemble these organs in Autolytus. There is, too, an absence of a well-developed external cuticular skeleton, so that the absence of a true jointing in the appendages is noticeable. Judging from figures, the terminal claws of the legs might be compared with the setæ of the annelid parapodium.

On the whole, Peripatus cannot be placed beyond question in the Arthropodan phylum, and it is doubtful if it would have been placed there were it not for the presence of tracheæ.

[12] The internal acicular teeth can hardly be regarded as appendages.

[13] I prefer to use the term Malacopoda for this group, because it is the oldest, being given by Blanchard in 1847. Onychophora of Grube dates from 1853, Protracheata was given by Mosely in 1874. The failure of Blanchard to recognize all points of structure does not invalidate his name.

As we have already pointed out the existence of three different kinds of tracheæ which cannot be traced to a common origin, it is barely possible that those of Peripatus and the other "Tracheates" are not strictly homologous.

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